

STRUCTURE, FUNCTION, AND VARIATION IN THE HINDLIMB
MUSCLES OF THE *MARGARORNIS* ASSEMBLAGE
(AVES: PASSERIFORMES: FURNARIIDAE)DAVID WYSS RUDGE¹ROBERT J. RAIKOW¹

Research Associate, Section of Birds

ABSTRACT

We dissected the hindlimb musculature in twenty specimens of five species of scansorial birds in the passerine family Furnariidae, genera *Margarornis*, *Premnornis*, *Premnoplex*, and *Roraimia* (collectively known as treerunners). The purposes of the study are: (1) to provide a complete description of the treerunners' hindlimb muscles, (2) to account functionally for any distinctive muscle variations in relation to the birds' scansorial habit, and (3) to assess the amount and types of individual variation present. Treerunners exhibit several myological variations that appear to be adaptive for tree climbing, but they are less highly specialized for this habit than are the Dendrocolaptinae. The frequency of individual variation in hindlimb muscles is low, in conformity with other passerine species. We also show that the treerunners exhibit the three hindlimb myological characters suggested as diagnostic for the Passeriformes by Raikow (1982).

INTRODUCTION

The *Margarornis* complex (treerunners and barbtails, hereafter collectively referred to as "treerunners") is a group of small, scansorial birds that inhabit northern South America and Central America. They are members of the family Furnariidae, subfamily Furnariinae, which are collectively called ovenbirds (Sibley and Monroe, 1990:405-6). The *Margarornis* assemblage includes: the Fulvous-dotted Treerunner (*Margarornis stellatus*), the Pearled Treerunner (*Margarornis squamiger*), the Ruddy Treerunner (*Margarornis rubiginosus*), the Rusty-winged Barbtail (*Premnornis guttuligera*), the Spotted Barbtail (*Premnoplex brunnescens*), and the Roraimian Barbtail (*Roraimia adusta*). The Beautiful Treerunner (*Margarornis bellulus*) and the Spotted Barbtail (*Premnoplex tatei*) were recognized by Vaurie (1980) as being conspecific with *Margarornis squamiger* and *Premnoplex brunnescens*, respectively, although Sibley and Monroe (1990) listed them as species. These forms have traditionally been allied on the basis of similar plumages and scansorial (i.e., tree trunk climbing) foraging habits, which are comparable to those of the Dendrocolaptinae (commonly known as woodcreepers).

The present paper is part of an ongoing cladistic analysis aimed at resolving the relationships of the Furnariinae and Dendrocolaptinae through the study of comparative hindlimb myology. In the present paper, we describe the hindlimb musculature of the *Margarornis* assemblage, with an emphasis on myological variation and the extent to which it may be explained in terms of function. In Rudge and Raikow (1992), we address the phylogenetic questions raised by this study.

¹ Department of Biological Sciences, University of Pittsburgh, Pittsburgh, PA 15260.
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Specific Aims

In this paper we examine representatives of all four genera of the treerunner assemblage, by means of comparative hindlimb myology, to address the following questions: (1) What modifications in treerunners are correlated with their scanorial habit, and how do they compare with those found in woodcreepers? The functional value of the distinctive myological variations found in this study will be analyzed with respect to these questions; (2) What kind of individual variation occurs in the hindlimb musculature of the *Margarornis* assemblage? This question will be examined in the context of a recent review of passerine myological variation (Raikow et al., 1990); and, (3) Does the hindlimb musculature of the *Margarornis* assemblage support the technical diagnosis of the Passeriformes? (Raikow, 1982).

MATERIALS AND METHODS

Twenty specimens of five species of birds preserved in ethanol were dissected. *Margarornis stellatus* was unavailable in museum collections. Sample sizes and catalog numbers are given below in parentheses, with abbreviations for museums from which specimens were borrowed as follows: FM, Field Museum of Natural History; LSU, Louisiana State University Museum of Natural Science; AMNH, American Museum of Natural History: *Margarornis rubiginosus* Lawrence (2: LSU/JPO 2289, LSU 64786); *Margarornis squamiger* (d'Orbigny and Lafresnaye) (5: LSU 60811, LSU 75008, LSU 79559, LSU 79560, LSU 331197); *Premnoplex brunnescens* (Sclater) (7: FM 321530, FM 321531, LSU 70631, LSU 75010, LSU 85962, LSU 89447, LSU 95543); *Premnornis guttuligera* (Sclater) (5: LSU 83865, LSU 89444, LSU 89445, LSU 107624, LSU 107625); *Roraimia adusta* (Salvin and Godman) (1: AMNH 7685).

Dissections were made with a Wild stereomicroscope at magnifications of $6\times$, $12\times$, and $25\times$. Iodine stain (Bock and Shear, 1972) was used to enhance visibility of muscle fibers. Preliminary drawings were prepared with the aid of a camera lucida microscope attachment. Abbreviations for Fig. 1–9 are as follows: CF, caudofemoralis; EA, extended area of the origin of M. flexor cruris medialis; EDL, extensor digitorum longus; FB, fibularis brevis; FCRLA, flexor cruris lateralis pars accessoria; FCRLP, flexor cruris lateralis pars pelvica; FCRM, flexor cruris medialis; FDL, flexor digitorum longus; FIB, head of the fibula; FL, fibularis longus; FPD3, flexor perforatus digiti III; FPD4, flexor perforatus digiti IV; FPPD2, flexor perforans et perforatus digiti II; FPPD3, flexor perforans et perforatus digiti III; FTED, femorotibialis externus pars distalis; FTEP, femorotibialis externus pars proximalis; FTI, femorotibialis internus; FTM, femorotibialis medius; GI, gastrocnemius pars intermedia; GL, gastrocnemius pars lateralis; GM, gastrocnemius pars medialis; ICR, iliotibialis cranialis; IF, iliofibularis; IFI, iliofemoralis internus; ILPO, iliotibialis lateralis pars postacetabularis; ILPR, iliotibialis lateralis pars preacetabularis; ITCA, iliotrochantericus caudalis; ITCR, iliotrochantericus cranialis; LI, lumbricalis pars intermedia; LL, lumbricalis pars lateralis; LM, lumbricalis pars medialis; LOBE, tibial lobe; OM, obturatorius medialis; PIF, pubo–ischio–femoralis; PIFCA, pubo–ischio–femoralis pars caudalis; PL, plantaris; TCR, tibialis cranialis. Anatomical nomenclature follows Baumel et al. (1979).

Each muscle was dissected through the entire series of specimens to allow direct comparison between the species. *Margarornis squamiger* was the reference species. A full description of each muscle in that species is first given, then compared with the same muscle in the other species.

Under "Comparison," we describe interspecific variation in arrangement, shape, size, or proportions of the muscle. We exclude slight differences in shape or size that are presumably the result of non-biological causes.

We classify intraspecific differences under "Individual variation" according to the categories provided by Raikow et al. (1990). We found examples of three of the five types they recognize: (1) minor variations (slight differences in shape, size, position, or proportions of a muscle that reflect nutritional differences, disease, effects of fixation, etc.), (2) singular variations (distinctive variations, not known to occur in other species), and (3) mimicking variations (variations atypical in one species that mimic a condition characteristic of another).

DESCRIPTIONS OF HINDLIMB MUSCLES

Muscles of the Thigh

M. iliotibialis cranialis (ICR) (Fig. 1, 2, 3)

M. squamiger.—This strap-shaped, parallel-fibered muscle forms the cranial border of the thigh. It is slightly wider at its origin, and passes distad to the

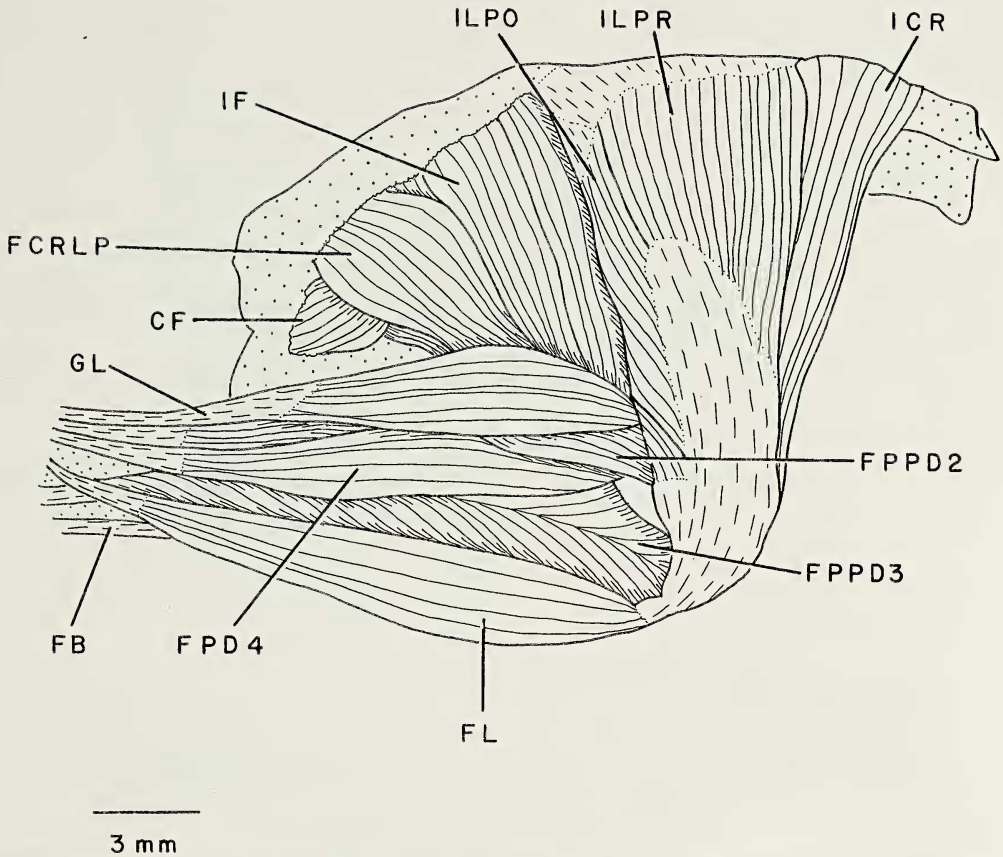


Fig. 1.—Lateral view of the superficial muscles of the thigh and crus in *Margarornis squamiger* LSU 79560. Abbreviations for Fig. 1–9 are given in Materials and Methods.

craniomedial surface of the thigh. Along its caudal edge it is overlain by the cranial border of *M. iliotibialis lateralis*.

Origin.—A single, fleshy head arises from the spinous processes of the last two free dorsal vertebrae caudal to the cranial border of the dorsal iliac crest, and continues for a short distance onto the cranioventral margin of the preacetabular ilium. Caudally the origin slightly overlaps the cranial border of *M. iliotrochantericus* caudalis.

Insertion.—The muscle inserts fleshy (1) on the distal one-fourth to one-half of the belly of *M. femorotibialis internus*, and (2) on the medial side of the head of the tibiotarsus onto the medial cnemial crest and the patellar ligament, where it is overlain by the origin of *M. gastrocnemius* pars medialis.

Comparison.—No interspecific variation was found in this muscle.

Individual variation.—None.

***M. iliotibialis lateralis* (ILPR, ILPO) (Fig. 1, 2)**

M. squamiger.—This large, triangular muscle occupies the lateral surface of the thigh, and lacks an acetabular gap. Two portions of the muscle are distinguished by their positions relative to the femur:

Pars preacetabularis (ILPR) is a large, flat, triangular component of the muscle that lies cranial and superficial to the femur, completely covering *Mm. iliotro-*

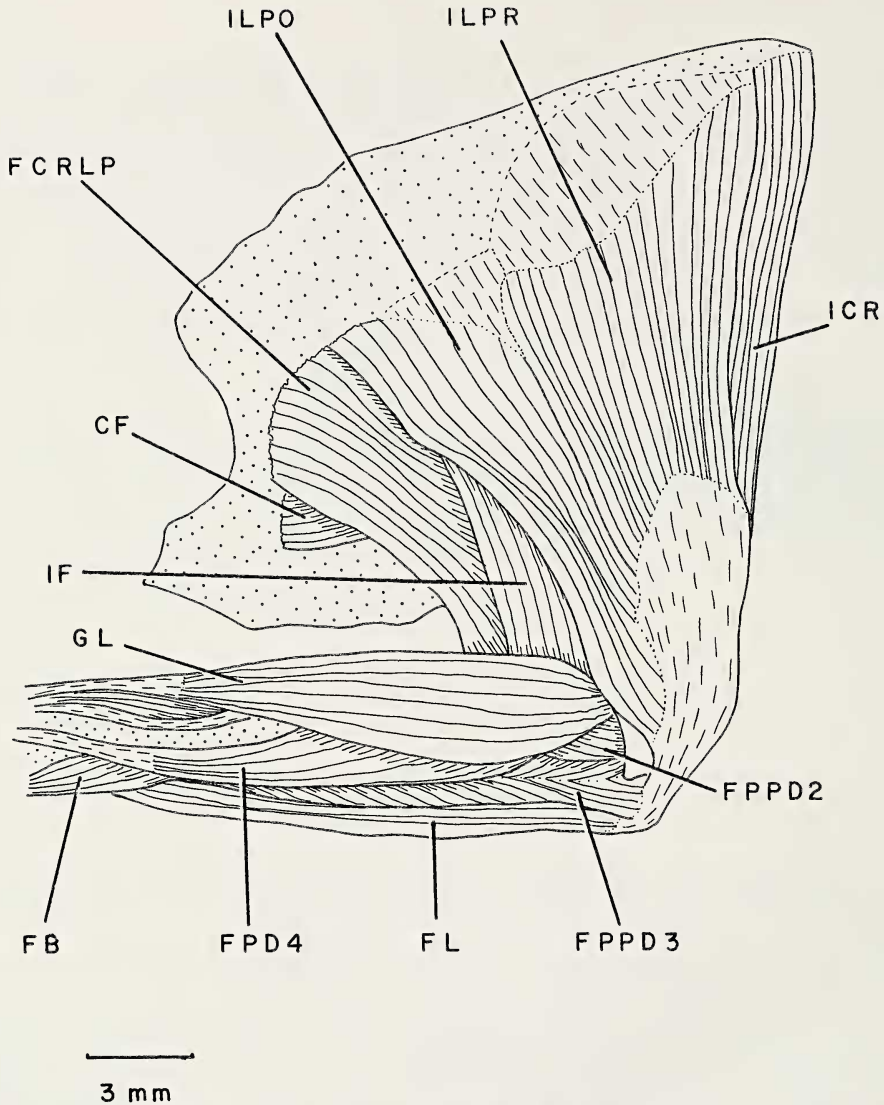


Fig. 2.—Lateral view of the superficial muscles of the thigh and crus in *Premnoplex brunnescens* FM 321531.

chantericus cranialis, iliotrochantericus medius, femorotibialis medius, and femorotibialis externus. It arises by a broad aponeurosis from the dorsal iliac crest (superficial to *M. iliotrochantericus caudalis*), and is continuous along its caudal border with the origin of the postacetabular portion of this muscle. It then passes both laterad over the surface of *M. femorotibialis externus* to contribute to the lateral aponeurosis, applied tightly to the surface of this muscle; and mediodistad, its most cranial fibers inserting tendinously on the patellar ligament.

Pars postacetabularis (ILPO) is a narrow, strap-shaped component that lies caudal to, but is continuous with the preacetabular portion. It arises tendinously from the caudalmost portion of the dorsal iliac crest and adjacent surface of the

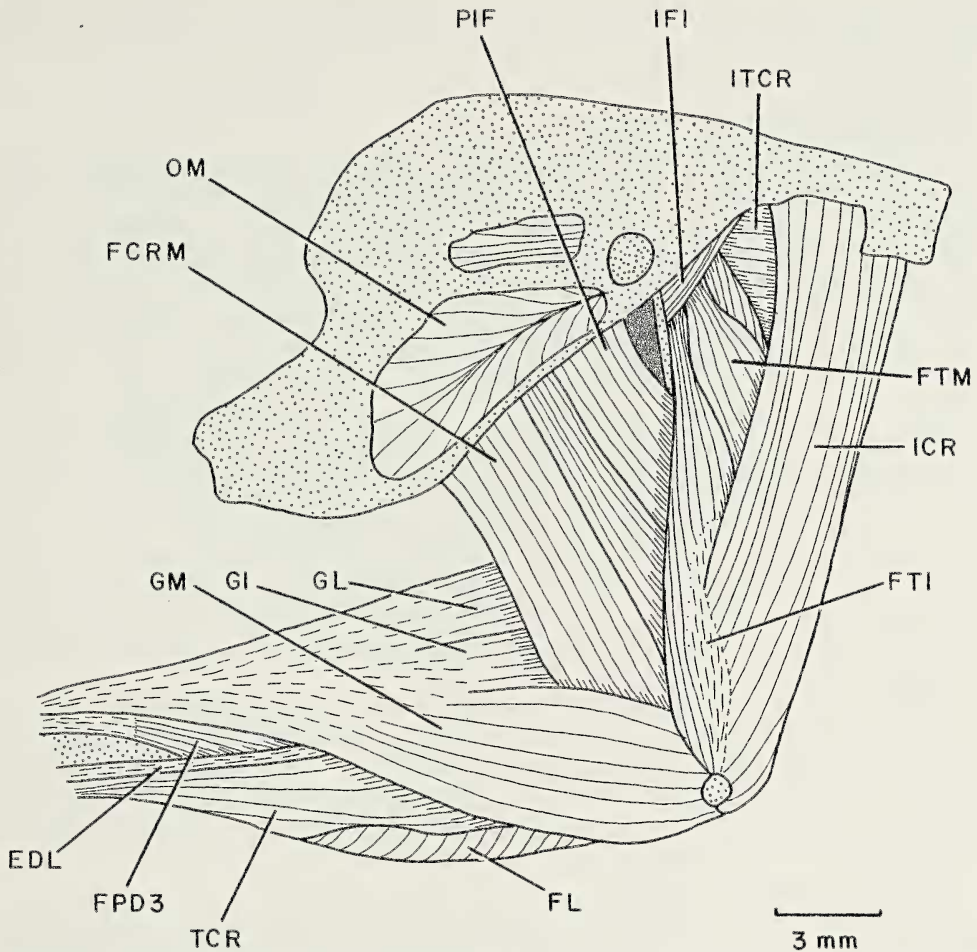


Fig. 3.—Medial view of the superficial muscles of the thigh and crus in *Margarornis squamiger* FM 331197.

postacetabular iliac wing, superficial to the origin of *M. ilioprochantericus caudalis* along its caudoventral margin, and to the origin of *M. iliofibularis* along its cranial border. It becomes fleshy at approximately the level of the *M. ischiofemoralis* insertion on the femur, and extends craniodistad over the cranialmost portion of *M. iliofibularis* to insert by tendinous fibers onto the caudolateral surface of *M. femorotibialis externus*, contributing to the lateral aponeurosis. The fleshy part of this portion ends well above its insertion, making the insertion of *M. femorotibialis externus* visible deep to it.

Comparison.—A marked reduction in the caudal margin of the postacetabular portion was found in all specimens of *Margarornis squamiger* and *M. rubiginosus* (Fig. 1). This is in contrast to *Roraimia adusta*, *Premnornis guttuligera*, and *Premnoplex brunnescens* (Fig. 2), where the postacetabular portion remains well developed, its origin extending across the origin of *M. iliofibularis* to the cranialmost portion of the origin of *M. flexor cruris lateralis pars pelvica*. In *Premnoplex brunnescens* the fleshy part of the postacetabular portion extended much farther

distad than in the other species, obscuring the insertion of *M. femorotibialis externus* (Fig. 2).

Individual variation.—None.

***M. iliofibularis* (IF) (Fig. 1, 2, 4, 6)**

M. squamiger.—This muscle lies in the caudolateral region of the thigh, deep to *M. iliotibialis lateralis pars postacetabularis* and caudal to the femur. It is shaped like an elongated triangle, with its origin forming a narrow base and the tendon of insertion arising at its apex, in the distal one-fifth of the muscle. The muscle is divided into two portions, corresponding to the cranial and caudal heads observed in *Eurylaimus* by Raikow (1987:11). These heads are fused throughout the length of the muscle, as in most passerines, and their fibers converge to form a single belly. The caudal portion extends only four-fifths the length of the cranial portion.

Origin.—The cranial portion arises mostly fleshy along the dorsolateral iliac crest; it begins aponeurotically at its cranial end from the caudal end of the dorsal iliac crest, and overlies the caudal margin of *M. iliotrochantericus caudalis*, and the cranial end of the dorsolateral iliac crest overlying the antitrochanter, deep to the origin of the postacetabular portion of *M. iliotibialis lateralis*. The fleshy cranial border of this origin lies superficial to the head of the femur, partially overlying the insertion tendon of *M. iliotrochantericus caudalis*. The caudal portion arises fleshy from the dorsolateral iliac crest, continuous with the cranial portion.

Insertion.—These two portions, which are nearly indistinguishable at their origin, become more distinct as the muscle passes distad, their fibers converging on a stout tendon which continues through the iliofibularis loop (see below) and then medial to the lateral head of *M. flexor hallucis longus* and lateral to *M. flexor digitorum longus* before inserting on the caudolateral surface of the fibular shaft.

Comparison.—No interspecific variation was found in this muscle.

Individual variation.—None.

Ansa m. iliofibularis (iliofibularis loop).—This tendinous structure at the base of the knee joint consists of three “arms” that house the *M. iliofibularis* insertion tendon. The proximal femoral arm arises on the lateral surface of the femoral shaft proximal to the origin of *M. gastrocnemius pars lateralis* and lateral to the insertion of *M. flexor cruris lateralis pars accessoria*. The distal femoral arm arises on the lateral aspect of the femur distal to the proximal arm, in common with the origin tendon of *M. gastrocnemius pars lateralis*. The fibular arm arises from the lateral surface of the fibular shaft just distal to the head of the fibula. It is fused with the tendon of the origin of the lateral head of *M. flexor hallucis longus*.

***M. iliotrochantericus caudalis* (ITCA) (Fig. 4)**

M. squamiger.—This is a large muscle occupying the dorsal iliac fossa (Fossa iliaca dorsalis) on the laterodorsal surface of the preacetabular iliac wing. It is nearly oval in shape and asymmetrically fan-shaped in its fiber architecture. The fibers converge caudad on a wide, flat tendon. The muscle’s ventral margin abuts *M. iliotrochantericus cranialis* (along the latter’s dorsal border) and completely overlies *M. iliotrochantericus medius*.

Origin.—The muscle arises fleshy from the surface of the dorsal iliac fossa and the dorsal iliac crest.

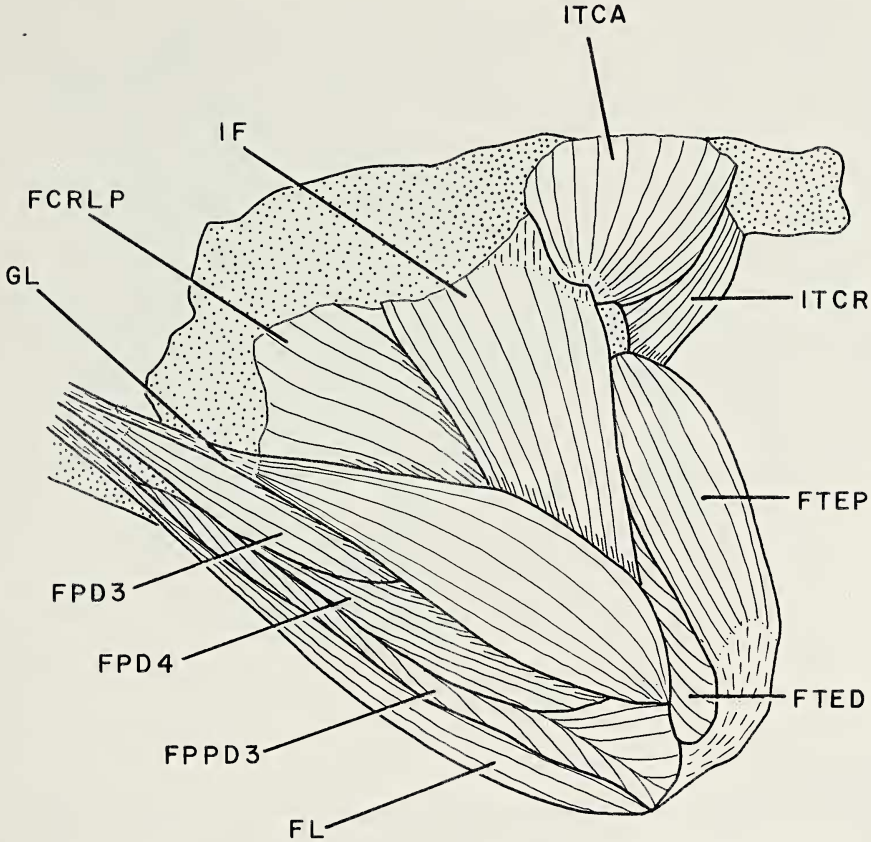
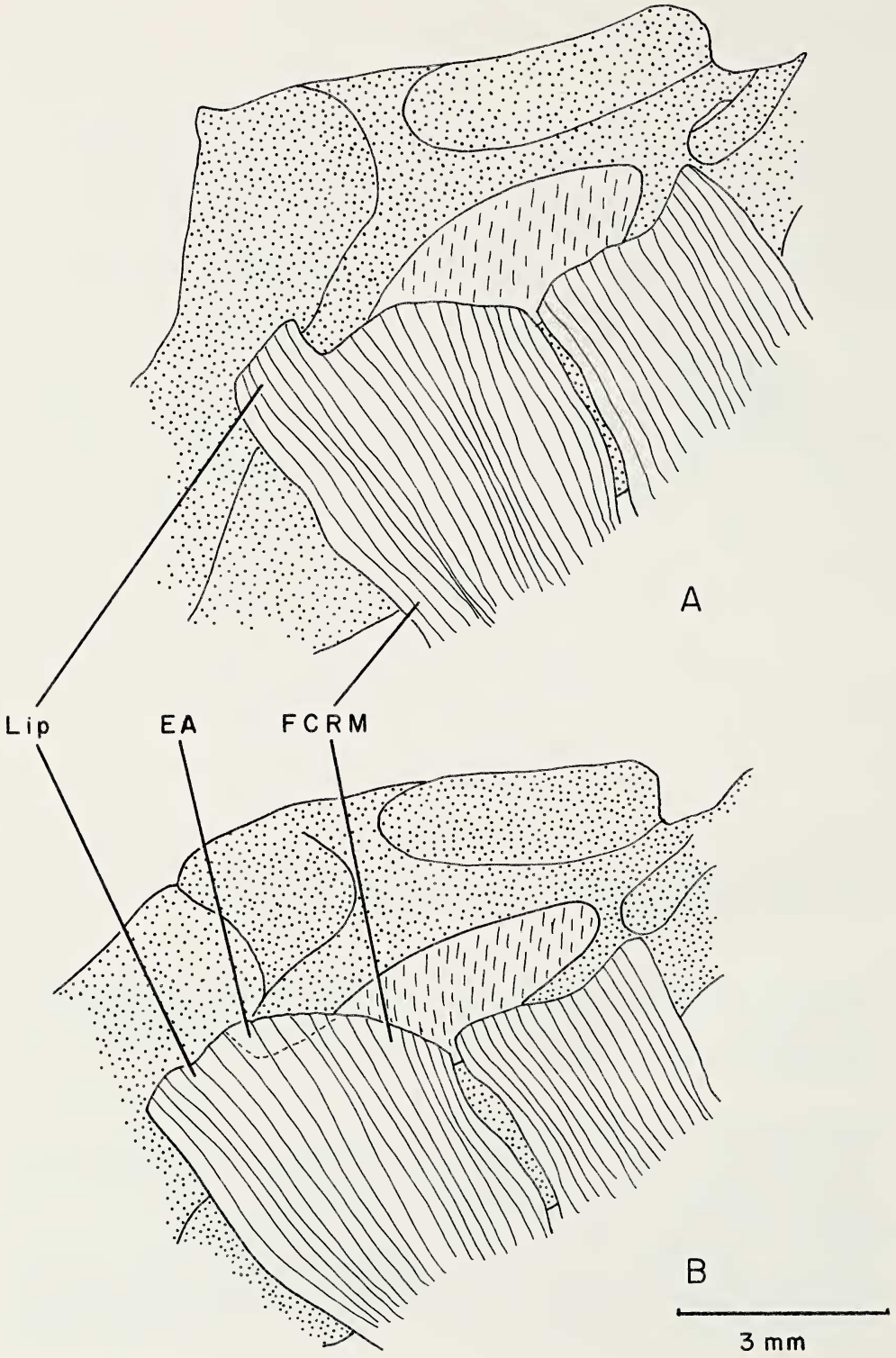


Fig. 4.—Lateral view of the muscles of the right thigh and crus in *Roraimia adusta* AMNH 7685. Mm. iliotibialis cranialis (ICR) and iliotibialis lateralis (IL) have been removed.

Insertion.—The fibers converge caudad onto a wide tendon inserting on the lateral surface of the proximal end of the femur just distal to the trochanter.
Comparison.—No interspecific variation was found in this muscle.
Individual variation.—None.

M. iliotrochantericus cranialis (ITCR) (Fig. 3, 4)

M. squamiger.—This flat, triangular muscle lies deep to M. iliotrochantericus caudalis. It is generally thicker along its cranial margin.
Origin.—This muscle arises fleshy from the cranioventral margin of the preacetabular ilium and aponeurotically at its extreme ventral margin.
Insertion.—The belly of this muscle is entirely separate from M. iliotrochantericus medius. It narrows as it passes to its short tendinous insertion on the cranioventral surface of the proximal end of the femur. The insertion tendon passes



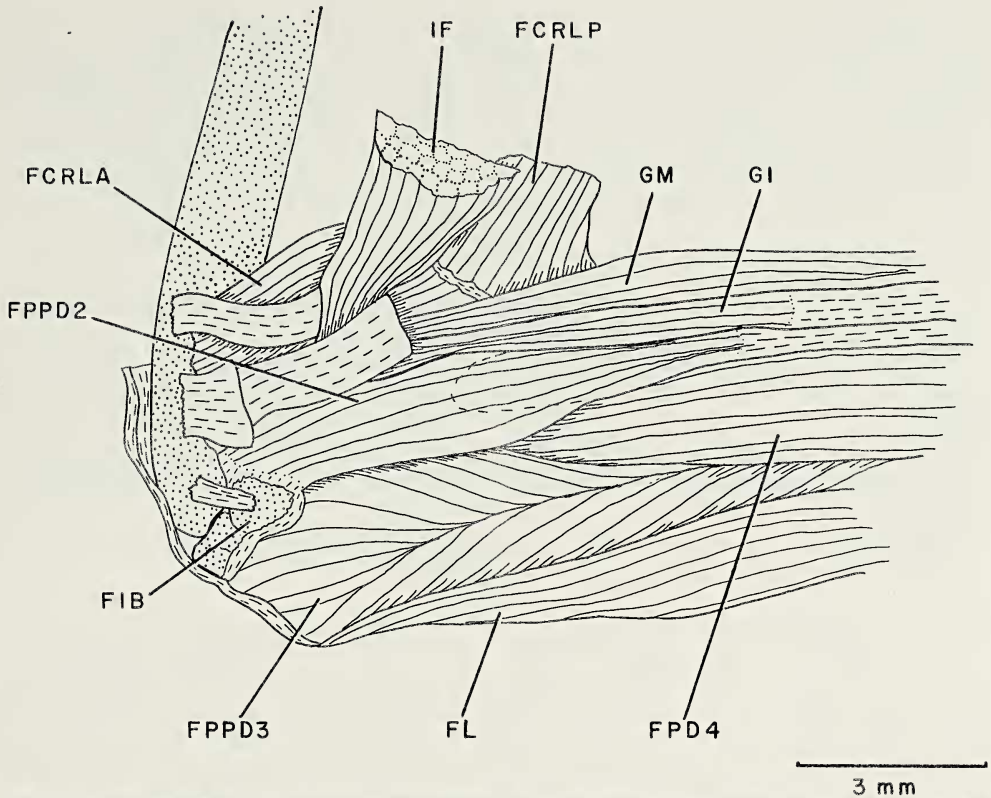


Fig. 6.—Origin of *M. flexor perforans et perforatus digiti II* (FPPD2) in *Premnoplex brunnescens* FM 321531, showing the origin in part from the head of the fibula.

distad to the tendinous insertion of *M. iliotrochantericus medius*, exhibiting a partial fusion with the latter along its cranial border.

Comparison.—No interspecific variation was found in this muscle.

Individual variation.—None.

M. iliotrochantericus medius

M. squamiger.—This is a small, strap-shaped muscle that lies between *Mm. iliotrochantericus caudalis* and *iliotrochantericus cranialis*.

Origin.—This muscle arises fleshy from the cranioventral margin of the preacetabular ilium and extends caudal to the origin of *M. iliotrochantericus cranialis*.

Insertion.—The belly of this muscle is entirely separate from *M. iliotrochantericus cranialis*. It inserts by a narrow tendon on the craniolateral surface of the proximal end of the femur at the level of the *M. ischiofemoralis* insertion. The insertion tendon fuses with that of *M. iliotrochantericus cranialis* along the latter's caudal border.

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Fig. 5.—Origin of *M. flexor cruris medialis* (FCRM) illustrating: (A) the presence of a “lip” in *Margarornis rubiginosus* LSU/JPO 2289, and (B) the hypertrophic origin found in *M. squamiger* LSU 75008.

Comparison.—No interspecific variation was found in this muscle.

Individual variation.—All of the specimens studied exhibit a clear separation between Mm. ilioprochantericus cranialis and ilioprochantericus medius, with the exception of one specimen of *Premnoplex brunescens* (LSU 89447), which bilaterally exhibited partial fusion of these muscles. This fused condition is characteristic of some dendrocolaptids as well as some furnariids (Raikow, personal communication), and thus in this specimen is a “mimicking” variation.

M. iliofemoralis internus (IFI) (Fig. 3)

M. squamiger.—This is a small, strap-shaped, nearly parallel-fibered muscle that fans out slightly at the point of insertion.

Origin.—The muscle arises fleshy from the ventral margin of the preacetabular ilium at a point just caudal and adjacent to the origin of M. ilioprochantericus medius.

Insertion.—The muscle passes caudodistad to insert fleshy on the medial surface of the proximocaudal end of the femur, proximal to the origin of M. femorotibialis internus.

Comparison.—No interspecific variation was found in this muscle.

Individual variation.—None.

M. femorotibialis externus et medius (FTEP, FTED, FTM) (Fig. 3, 4)

M. squamiger.—Mm. femorotibialis externus and femorotibialis medius are separate muscles in many birds, but their extensive fusion in the species of this study allows their description as a single complex. The muscle arises from the cranial, medial, and lateral surfaces of the femoral shaft, inserting via a heavy tendon (which incorporates the patella) onto the head of the tibiotarsus. The two portions of the muscle are treated separately below.

M. femorotibialis externus (FTEP, FTED):

M. squamiger.—M. femorotibialis externus lies on the lateral surface of the thigh deep to the central portion of M. ilioprochantericus lateralis, and overlies the lateral aspect of the femoral shaft. It is composed of two parts.

Pars proximalis (FTEP) is incompletely separated along its cranial margin from M. femorotibialis medius. It arises fleshy from the shaft of the femur beginning just proximal to the level of insertion of M. ischiofemoralis. Along its distal surface the muscle gives rise to the lateral superficial portion of the patellar tendon.

Pars distalis (FTED) is an elongate, asymmetrically fan-shaped muscle that arises mostly fleshy from the caudolateral surface of the femoral shaft and becomes tendinous along its proximal surface at about the level of insertion of M. caudofemoralis. It continues distad to form a flat tendon that becomes the lateral deep layer of the patellar tendon, which inserts on the lateral cnemial and patellar crests of the head of the tibiotarsus.

Comparison.—No interspecific variation was found in this muscle.

Individual variation.—None.

M. femorotibialis medius (FTM):

M. squamiger.—M. femorotibialis medius (FTM) is a thick, elongated muscle completely overlying the cranial aspect of the femur. Along its lateral surface it lies deep to M. ilioprochantericus cranialis and to the preacetabular belly of M. ilioprochantericus

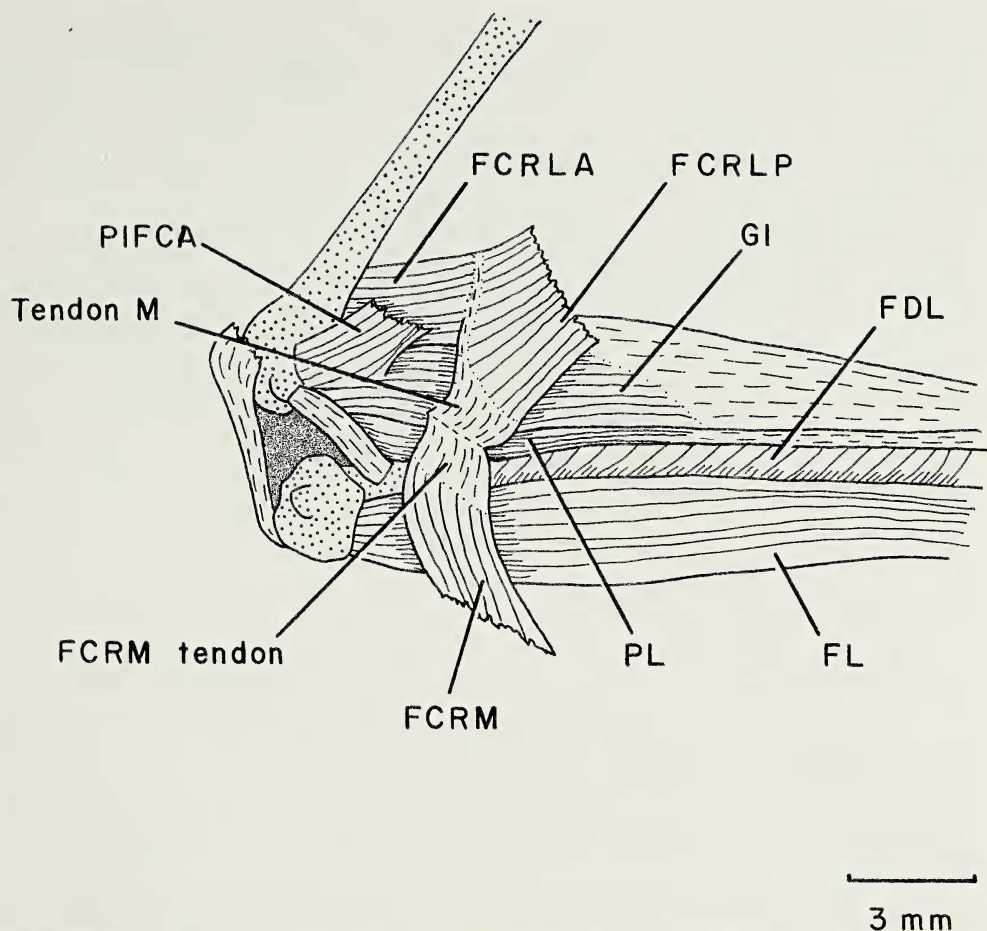


Fig. 7.—Relationship of *M. flexor cruris lateralis pars pelvica* (FCRLP) to Tendon M in *Margarornis squamiger* LSU 79559.

lateralis. Along its caudomedial surface it lies deep to *M. femorotibialis internus*. It is composed of two parts.

Pars proximalis: This is a thick muscle overlying the cranial surface of the femur, which is incompletely separated from *M. femorotibialis externus* pars proximalis along its lateral surface. It arises fleshy for nearly the entire length of the femur along its craniomedial surface, and becomes tendinous from the trochanter and curves mediad as it passes distad. Distally this muscle gives rise to the cranial and medial superficial portions of the patellar tendon that jointly insert onto the patellar crest of the tibiotarsus.

Pars distalis: This is a small, elongate, triangular muscle on the distomedial surface of the femur. Its belly lies superficial to the medial surface of Pars proximalis. It arises mostly fleshy along the medial surface of the femoral shaft, becoming tendinous at approximately the midpoint of the femur. The muscle continues distad, forming a flat tendon which is joined by the tendon of Pars proximalis as it inserts on the extreme craniomedial surface of the patellar tendon.

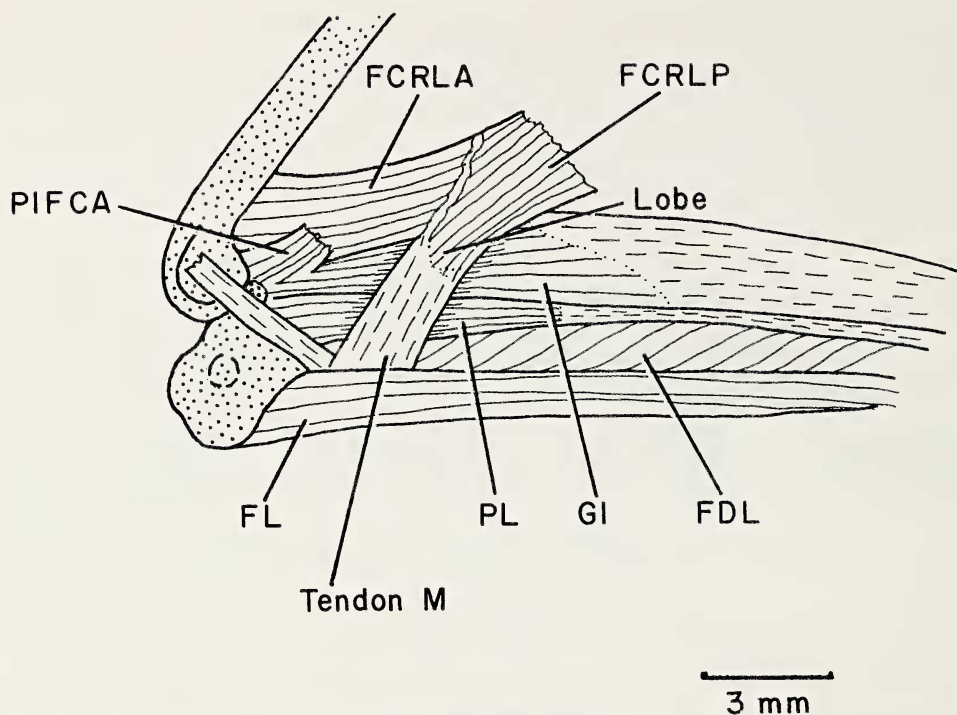


Fig. 8.—Extension of a “lobe” from *M. flexor cruris lateralis pars pelvica* (FCRLP) into Tendon M in *Premnoplex brunnescens* LSU 89447.

Comparison.—No interspecific variation was found in this muscle.

Individual variation.—None.

M. femorotibialis internus (FTI) (Fig. 3)

M. squamiger.—This is a large muscle lying on the medial surface of the thigh, over the femur. Its distal portion lies deep to the insertion of *M. iliotibialis cranialis* (see above).

Origin.—The muscle arises fleshy along the length of the femoral shaft, beginning along its proximal surface just cranial to the insertion of *M. iliofemoralis internus*. Its narrow belly widens distally as its fibers converge caudodistally to insert partly fleshy and partly by a short tendon that arises on the medial surface of the muscle.

Insertion.—The distal end of the muscle passes over the medial collateral ligament (Ligamentum collaterale mediale) to insert onto the medial surface of a large bony process on the medial side of the tibiotarsus, caudal to the cranial cnemial crest and deep to the origin of *M. gastrocnemius medialis*.

Comparison.—No interspecific variation was found in this muscle.

Individual variation.—None.

M. flexor cruris lateralis (FCRLP, FCRLA) (Fig. 1, 2, 4, 6, 7, 8)

M. squamiger.—This large, rectangular muscle forms the caudolateral aspect of the thigh, and lies caudad to *M. iliofibularis* and superficial to *Mm. caudofemoralis*, *ischiofemoralis*, and *flexor cruris medialis*. It is divided into two parts separated by a raphe.

Pars pelvica (FCRLP): The proximal portion of the muscle is nearly parallel-fibered throughout its length, and its distinctly thicker along its cranial border. It arises mostly fleshy from the caudal end of the dorsolateral iliac crest and the adjacent lateral surface of the terminal process of the ilium, beginning tendinous along its cranial border. The caudal end of the origin arises from the membrana iliocaudalis, a sheet of connective tissue associated with the first one or two caudal vertebrae, and extends beyond the ilium. Pars pelvica passes distad into the proximomedial portion of the shank, and ends at the raphe separating it from Pars accessoria. The raphe arises on the cranial surface of the muscle and passes around the medial surface of the belly. The caudal half of Pars pelvica continues caudad to the raphe and Pars accessoria, forming a fleshy "tibial lobe" that gives rise, in part, to Tendon M. On the lateral surface of the distal end of Pars pelvica, the raphe also gives rise to a short extension, Tendon G, which passes distad to merge with the dorsal margin of M. gastrocnemius pars intermedia. (Both of these extensions of the raphe are discussed in further detail below.)

Pars accessoria (FCRLA): This distal, parallel-fibered portion of the muscle serves to connect Pars pelvica to the femoral shaft. Its ventral margin lies adjacent to the dorsal surface of M. gastrocnemius pars intermedia. The fibers of the two muscles run in parallel such that, when the crus is flexed, the two lie together and appear fused. It arises fleshy from the raphe as a continuation of Pars pelvica and passes craniad and at an angle to the former muscle, to insert fleshy on the distolateral surface of the femoral shaft, deep to the origin of the proximal arm of the iliofibularis loop. The insertion extends distomedial over the caudal surface of the femoral shaft. At the medial femoral condyle, the insertion of this muscle merges with the origin of M. gastrocnemius pars intermedia.

Raphe: The raphe separating Pars pelvica from Pars accessoria gives rise to two tendinous extensions. Tendon G is a short, stout tendon that arises as a continuation of the raphe on the lateral side of the muscle, which turns distad to merge with the dorsal margin of the distal third of the belly of M. gastrocnemius pars intermedia. Tendon M is a wide, flat tendon that arises from the distal half of the raphe on the medial side of M. flexor cruris lateralis from about the midpoint of Pars accessoria to the caudal margin of Pars pelvica. Distally, Tendon M fuses with the lateral surface of the M. flexor cruris medialis tendon, providing an effective insertion for Pars pelvica on the tibia.

Comparison.—Tendon M was found to originate entirely from the tibial lobe of Pars pelvica in *Premnornis guttuligera* and *Premnoplex brunnescens* (Fig. 8).

Individual variation.—None.

M. flexor cruris medialis (FCRM) (Fig. 3, 5, 7)

M. squamiger.—This strap-shaped, nearly parallel-fibered muscle lies in the caudolateral region of the thigh deep to M. flexor cruris lateralis and is superficial to almost the entire caudal half of the lateral surface of the ischiopubic fenestra. It narrows slightly toward its insertion on the tibial shaft.

Origin.—The muscle arises fleshy from the lateral surface of the ischium along the dorsal surface of the Ala ischii from a point at about the middle of the ischiopubic fenestra caudad to the dorsal rim of the ischiopubic fenestra. The caudal 1 mm of the origin forms a characteristic "lip" which extends dorsad over the rim of the fenestra, approximately 0.5 mm from the membrana iliocaudalis, beyond the terminal ischiatic process.

Insertion.—The muscle passes distad medial to M. flexor cruris lateralis and lateral to M. gastrocnemius pars medialis. At approximately the level of M.

gastrocnemius pars intermedia, the muscle gives rise to a wide, flat tendon that inserts on the medial surface of the tibial shaft superficial to the insertion of the medial collateral ligament. Along its lateral surface, the tendon is joined by Tendon M of *M. flexor cruris lateralis* (see above).

Comparison.—No interspecific variation was found in this muscle.

Individual variation.—None.

***M. caudofemoralis* (CF) (Fig. 1, 2)**

M. squamiger.—This elongate, flat, spindle-shaped muscle extends from the femur, through the caudal half of the thigh, to the undersurface of the pygostyle.

Origin.—The muscle arises by a flat tendon on the caudolateral surface of the femoral shaft slightly distad to the insertion of *M. ischiofemoralis*. The tendon of origin of this muscle is short and its fleshy belly arises proximal to the cranial margin of *M. flexor cruris lateralis*. The belly of the muscle widens distinctly as it passes caudad, superficial to *Mm. ischiofemoralis* and *flexor cruris medialis*, and deep to *Mm. flexor cruris lateralis* and *iliofibularis*.

Insertion.—The muscle continues distad into the tail region between *Mm. pubocaudalis internus* and *depressor caudae* to insert by a short, narrow tendon onto the disc of the pygostyle lateral to the insertion of *M. depressor caudae*, slightly craniomedially and mostly deep to the insertion of *M. pubocaudalis internus*.

Comparison.—No interspecific variation was found in this muscle.

Individual variation.—None.

M. ischiofemoralis

M. squamiger.—This is a large, asymmetrically fan-shaped muscle lying deep to *M. caudofemoralis*. Its caudal margin arises from a membrane passing across the caudal end of the pelvis from the *Processus terminalis ilii* to the *Processus terminalis ischii*.

Origin.—This muscle arises fleshy from the lateral surface (the *Lamina ischiadica*) of the ilium, caudal to the ilioischadic foramen; and from the ventral margin of the *Crista iliaca dorsolateralis* dorsal to the caudal half of the foramen. Ventrad, it arises from the *Ala ischii* caudal and ventral to that opening.

Insertion.—This muscle inserts by a stout tendon that arises on the craniolateral surface of the muscle as it narrows craniad on the lateral surface near the proximal end of the femur, at the level of the insertion of *Mm. iliotrochantericus cranialis* and *iliotrochantericus medius* and distal to the insertion of *M. obturatorius medialis*.

Comparison.—No interspecific variation was found in this muscle.

Individual variation.—None.

***M. obturatorius medialis* (OM) (Fig. 3)**

M. squamiger.—This large, flat, asymmetrically ovoid muscle occupies the ischiopubic fenestra of the pelvic girdle medial to the ischiopubic membrane. Its broadly bipennate belly is elongate and narrow, and extends slightly farther caudad at its ventral margin than at its more rounded dorsal margin.

Origin.—The muscle arises fleshy from the medial surfaces of the ischium and pubis that form the rim of the ischiopubic fenestra; dorsally and caudally from the medial surface of the *Ala ischii*; ventrally from the medial surface of the pubis.

Insertion.—A stout tendon of insertion arises deep within the muscle and passes, with some associated muscle fascicles, through the obturator foramen. It emerges on the lateral surface of the pelvic girdle, dorsal to *M. obturatorius lateralis pars ventralis* and just ventral to the antitrochanter, and continues craniolaterad to insert on the femoral trochanter dorsal and slightly cranial to the insertion of *M. obturatorius lateralis pars ventralis*.

Comparison.—No interspecific variation was found in this muscle.

Individual variation.—None.

M. obturatorius lateralis

M. squamiger.—This small muscle lies deep in the hip on the caudal aspect of the proximal end of the femur and, in many birds, consists of two separate bellies: *Pars dorsalis* and *Pars ventralis*. *Pars dorsalis* is absent in *M. squamiger*.

Pars ventralis: This short, parallel-fibered muscle runs alongside the insertion tendon of *M. obturatorius medialis* towards its insertion on the head of the femur.

Origin.—The muscle arises fleshy from the lateral surface of the *Corpus ischii* in the area of fusion with the pubis, and also from the ventral margin of the obturator foramen, a few fibers arising from the ventral lip of this opening.

Insertion.—The muscle passes craniodorsad, and runs nearly parallel to the insertion tendon of *M. obturatorius medialis*. It inserts fleshy on the caudal surface of the proximal end of the femur just distal to the latter muscle's insertion.

Comparison.—No interspecific variation was found in this muscle.

Individual variation.—None.

***M. pubo-ischio-femoralis* (PIF, PIFCR, PIFCA) (Fig. 3, 7, 8)**

M. squamiger.—As in other passerines, this thick muscle consists of two separate bellies that lie in a craniocaudal orientation (Raikow, 1982:440). *Pars cranialis* slightly overlaps *Pars caudalis*.

Pars cranialis (PIFCR) is a wide, parallel-fibered muscle that extends from the ischium to the femur. It arises mostly fleshy (along its lateral surface) from the *Corpus ischii* and the cranial end of the *Ala ischii* of the ischium, and follows the dorsal rim of the ischiopubic fenestra to about its midpoint. The muscle passes craniodistad to insert fleshy along the caudal face of the femoral shaft beginning proximally at the level of the *M. caudofemoralis* insertion and continuing distad to the level of the proximal arm of the iliofibularis loop on its lateral side. The muscle continues from its medial surface to a point just short of the medial femoral condyle; from its proximal surface, the muscle continues to the combined insertion of *Pars caudalis* and *M. gastrocnemius pars intermedia*.

Pars caudalis (PIFCA) is a narrow, almost parallel-fibered muscle lying caudal to and entirely separate from *Pars cranialis*. It arises by a wide, flat tendon from the ventral margin of the *Ala ischii* just caudal to the origin of *Pars cranialis* to a point deep to the cranial half of the origin of *M. flexor cruris medialis*. The tendon passes distad, widens and becomes fleshy at about the level of the pubis. The belly subsequently narrows slightly as it passes distad to fuse on the dorso-medial surface of *M. gastrocnemius pars intermedia*. Its most cranial fibers contribute to the tendinous origin of the latter onto the femoral shaft.

Comparison.—No interspecific variation was found in this muscle.

Individual variation.—None.

*Muscles of the Crus***M. tibialis cranialis (TCR) (Fig. 3)**

M. squamiger.—This large muscle lies on the cranial surface of the crus deep to *M. fibularis longus* and superficial to *M. extensor digitorum longus*. On the lateral side of the crus it lies cranial to *M. fibularis brevis*.

Origin.—This muscle arises by two heads which remain separate for most of the length of the muscle:

Caput tibiale: The tibial head arises fleshy from the lateral and cranial cnemial crests and the intervening patellar crest of the head of the tibiotarsus. This origin is tendinous from the medial aspect of the cranial cnemial crest. As the tibial head passes distad, its fibers converge upon the tendon of insertion. The fleshy belly of this muscle runs nearly three-fourths of the length of the crus.

Caput femorale: The femoral head arises by a short (ca. 1 mm), stout tendon from the apex of the lateral femoral condyle. It passes distad to merge with the tibial head, giving an overall bipennate arrangement.

Insertion.—The common tendon of insertion passes beneath the transverse ligament, crosses the intertarsal joint, and inserts on a bony elevation (the *Tuberositas m. tibialis cranialis*) on the proximocranial surface of the tarsometatarsus. The tendon is not ossified.

Comparison.—No interspecific variation was found in this muscle.

Individual variation.—None.

M. extensor digitorum longus (EDL) (Fig. 3)

M. squamiger.—This is the deepest muscle on the cranial surface of the crus, lying deep to *M. tibialis cranialis*. The belly is symmetrically bipennate at its origin, changes to unipennate for about half of its length, and extends approximately three-fourths of the length of the tibiotarsus.

Origin.—The muscle arises fleshy from the the patellar crest, the cranial cnemial crest, and also the lateral cnemial crest along the distal surface of the *Sulcus intercristalis*. The origin continues fleshy along the tibial shaft from its craniomedial surface, giving the origin a roughly symmetric, bipennate appearance. At about one-third of the length of the belly, this craniomedial origin converges on the tendon of insertion, from which point the muscle continues unipennate along its lateral surface. Shortly before the transverse ligament, the fibers of the lateral portion of the belly converge on the common tendon.

Insertion.—The tendon continues under the transverse ligament and then beneath the bony supratendinal bridge at the distal end of the tibiotarsus. From there it crosses the intertarsal joint. At the dorsoproximal end of the tarsometatarsus the tendon is held in place by an ossified loop, the *Retinaculum extensorium tarsometatarsi*. It then continues distad along the dorsal surface of the tarsometatarsus, medial to the insertion of *M. tibialis cranialis*. Near the distal end of the tarsometatarsus the tendon trifurcates, sending one branch to each of the three forward toes. Each branch passes along the dorsal surface of its respective digit to insert at the base of the ungual phalanx. Secondary attachments were not examined in detail. Throughout its length the tendon exhibits no sign of ossification.

Comparison.—No interspecific variation was found in this muscle.

Individual variation.—None.

M. fibularis longus (FL) (Fig. 1, 2, 3, 4, 6, 7, 8)

M. squamiger.—This is a well-developed muscle on the cranial surface of the crus, the cranial edge of which is superficial to *M. tibialis cranialis* and adjacent to *M. flexor perforans et perforatus digiti III*. The muscle is flat and roughly leaf shaped. It is asymmetrically bipennate, and is composed of two muscle masses that converge on a common central tendon.

Origin.—The muscle arises fleshy from the cranial and lateral cnemial crests, and from the patellar crest. In addition, there is an aponeurotic origin from the medial surface of the cranial cnemial crest at a point adjacent to the bony projection discussed under *M. femorotibialis internus*. The aponeurotic portion of the muscle continues for the length of the muscle, forming a tendinous sheath along the muscle's medial border superficial to *Mm. extensor digitorum longus* and *tibialis cranialis*. The fleshy lateral origin is larger.

Insertion.—The fleshy belly continues for about two-thirds of the length of the crus. Its central tendon continues distad and subsequently divides into two branches.

Short branch: The shorter, more caudal branch of the tendon extends distad to fuse with the proximolateral corner of the tibial cartilage.

Long branch: The longer branch continues distad across the lateral surface of the tibiotarsus, passes beneath a retinaculum, and continues superficial to the *M. fibularis brevis* tendon. It then crosses the intertarsal joint to the proximolateral surface of the head of the tarsometatarsus, where it continues distad in a groove formed along the caudolateral edge of the hypotarsus. At the distal end of the groove, the tendon passes beneath a tendinous retinaculum on its way to its fusion with the *M. flexor perforatus digiti III* tendon at a point about one-third of the length of the tarsometatarsus. Neither tendon exhibits ossification.

Comparison.—No interspecific variation was found in this muscle.

Individual variation.—None.

M. fibularis brevis (FB) (Fig. 1, 2)

M. squamiger.—This is a long, narrow, asymmetrically bipennate muscle that lies deep on the lateral surface of the crus.

Origin.—It arises fleshy from the craniolateral surface of the fibular shaft distal to the *M. iliofibularis* insertion, and from the craniolateral surface of the shaft of the tibiotarsus for most of its length. This corresponds to the "fibular head" discussed by Raikow (1976:785). There is no "tibial head" as has been described in some oscines (e.g., Raikow, 1977:100–102, 1978:22). The belly arises fleshy for nearly the entire length of the crus, from both the fibular shaft and the adjacent portions of the tibial shaft. These fibers converge distad upon a common tendon of insertion.

Insertion.—The tendon passes beneath an ossified loop, the Retinaculum *m. fibularis*, and deep to the long branch of the *fibularis longus* tendon, proximal to the lateral condyle. It then crosses the intertarsal joint turning slightly mediad to insert on the proximolateral corner of the tarsometatarsus. The tendon is not ossified.

Comparison.—No interspecific variation was found in this muscle.

Individual variation.—None.

M. gastrocnemius (GL, FI, GM) (Fig. 1, 2, 3, 4, 6, 7, 8)

M. squamiger.—This muscle consists of three separate bellies that contribute to a common tendon of insertion.

Pars lateralis (GL): This is the most superficial muscle on the dorsolateral surface of the crus. It is elongate and spindle shaped in appearance. It arises by a flat tendon that spreads out over the medial surface of the belly from the distolateral surface of the femoral shaft at a point just proximal to the lateral condyle. The tendon originates slightly distal to the proximal arm of the iliofibularis loop, itself forming a superficial layer of the distal femoral arm of this structure. The fleshy belly of this muscle extends slightly over half of the length of the tibial shaft. The tendon of insertion arises over the dorsal surface of the belly as it narrows distally, and joins with the tendons of the other bellies to form the common tendon of insertion of *M. gastrocnemius*.

Pars intermedia (GI): This is the smallest and most deeply situated of the three bellies. It consists of a narrow, elongated, and slightly spindle-shaped belly that extends from the femur less than half the length of the crus. The belly is essentially parallel fibered and flattened along its lateromedial surface. It arises partly fleshy and partly by short tendinous fibers from the caudodistal margin of the femoral shaft in the region of the Fossa poplitea and also from the lateral surface of the medial femoral condyle. A few tendinous fibers pass to the belly from the joint capsule. The middle portion of the origin lies just medial to and in close association with the insertion of *M. pubo-ischio-femoralis pars caudalis*. The dorsal boundary separating the origin of this muscle from *M. flexor cruris lateralis pars accessoria* is obscured by the presence of several muscle fascicles that arise from Tendon G of *M. flexor cruris lateralis* and extend to the femur. The belly extends approximately one-third of the length of the crus, giving rise to a tendon that joins with the tendons of the other bellies to form the common tendon of insertion. Tendon G enters at about the midpoint of the belly and contributes to the dorsal margin of the distal one-half of the belly and to the tendon of insertion.

Pars medialis (GM): This is the most superficial muscle on the medial surface of the crus. The belly is like that of other passerines, in which it is broad with a convex cranial margin. It arises fleshy from the medial surface of the cranial cnemial crest on the head of the tibiotarsus and from the distal and cranial surfaces of a bony projection discussed above under *M. femorotibialis internus*. The origin continues distad from the tibial shaft and also from the aponeurotic surface of the underlying *M. fibularis longus*. The belly of the muscle passes distad, and extends nearly two-thirds of the length of the crus before giving rise to a tendon on its medial surface which joins with the tendons of the other bellies to form the common tendon of insertion of *M. gastrocnemius*.

The tendon of insertion passes over the tibial cartilage and the hypotarsus, to the lateral and medial edges of which it has loose connections. Beyond the hypotarsus it turns laterad and spreads to an insertion on the low lateral plantar crest on the caudolateral surface of the tarsometatarsus. None of the tendons is ossified.

Comparison.—All specimens of *Premnornis guttuligera* and *Premnoplex brunescens* were found to have both deep and superficial heads for Pars medialis, some of which also were found to exhibit a patellar band (described by Raikow, 1987:18) to varying degrees. The single specimen of *Roraimia adusta* exhibited only one head. (On the *Margarornis* specimens, Pars medialis was removed before a determination of whether separate heads were present; but only one, *M. rubiginosus* LSU 64786, was found to have bilaterally a patellar band.)

Individual variation.—An interesting unilateral variation in Pars medialis was found in *Margarornis squamiger* LSU 75008 and LSU 79560, *Margarornis ru-*

biginosus LSU/JPO 2289, and *Premnoplex brunnescens* FM 321531, in which a separate tendon of origin was found deep to the origin of Pars medialis listed above. This represents a “singular” variation.

M. plantaris (PL) (Fig. 7, 8)

M. squamiger.—This small muscle lies in the caudomedial region of the crus, deep to the insertion tendon of M. flexor cruris medialis, medial to the origin of the medial head of M. flexor digitorum longus, and lateral to the medial collateral ligament. Its narrow, fan-shaped belly extends distad for one-fourth of the length of the crus.

Origin.—The muscle arises fleshy from the proximomedial surface of the head of the tibiotarsus.

Insertion.—The fine tendon of insertion arises as a superficial sheet over the distal part of the medial side of the belly. The tendon proceeds distad to its insertion on the proximomedial corner of the tibial cartilage and is nonossified throughout its length.

Comparison.—No interspecific variation was found in this muscle.

Individual variation.—None.

M. flexor perforans et perforatus digiti II (FPPD2) (Fig. 1, 2, 6)

M. squamiger.—This flat, narrow, fan-shaped muscle lies on the proximolateral surface of the crus between Mm. flexor perforans et perforatus digiti III and gastrocnemius pars lateralis. The belly extends about one-third of the length of the crus.

Origin.—The muscle arises fleshy from the laterodistal surface of the femur just proximal to the origin of M. gastrocnemius pars lateralis and the caudal edge of the lateral femoral condyle. The origin extends caudolaterad, along the ligamentum collaterale laterale, the lateral collateral ligament, onto the head of the fibula itself. A common raphe extends from this origin between Mm. flexor perforans et perforatus digiti II and flexor perforans et perforatus digiti III for a short distance over the surface of the latter muscle. The undersurface of the origin proximal to the lateral femoral condyle is tendinous and serves as a common origin tendon for M. flexor perforatus digiti II.

Insertion.—A fine tendon of insertion arises on the lateral surface of the belly and proceeds distad. It passes through the tibial cartilage and hypotarsus and continues along the plantar surface of the tarsus to the base of digit II. Upon emerging from the hypotarsus, the tendon entwines the M. flexor perforatus digiti II tendon, and passes superficial from a position initially medial to this latter tendon. At the distal end of the tarsometatarsus, the tendon becomes deep to the tendon of M. flexor perforatus digiti II as it passes deep to Metatarsal I on its way to the plantar surface of the second digit. Upon emergence, the tendon ensheathes the M. flexor digitorum longus branch tendon to digit II (described below), and continues distad. Near the distal end of phalanx I, the tendon bifurcates into a short elastic medial branch that inserts deep to the tendon of M. flexor digitorum longus, and a second branch that inserts lateral to this latter tendon on the ventral margin of the joint pulley of phalanx II. There is no sign of ossification in the tendon.

Comparison.—No interspecific variation was found in this muscle.

Individual variation.—None.

M. flexor perforans et perforatus digiti III (FPPD3) (Fig. 1, 2, 4, 6)

M. squamiger.—This muscle lies on the lateral surface of the crus, cranial to Mm. gastrocnemius pars lateralis and flexor perforans et perforatus digiti II, and caudal to M. fibularis longus. The proximal portion of this muscle is bipennate, and the distal part becomes unipennate at approximately the midpoint of the belly.

Origin.—The muscle arises by a short, flat tendon that spans the knee joint. Along its cranial surface the origin arises from the lateral edge of the tibiotarsus from the lateral cnemial crest. The origin arises caudad from the lateral femoral condyle in close association with the origins of Mm. flexor perforatus digiti II and flexor perforans et perforatus digiti II. The belly gives rise to a tendon that runs the length of the crus.

Insertion.—The tendon of insertion arises along the deep, lateral surface of the belly and passes through the tibial cartilage and hypotarsus to continue distad in the tendon bundle along the plantar surface of the tarsometatarsus. Upon emerging from the hypotarsus, the tendon entwines the M. flexor perforatus digiti III tendon, and passes superficial from a position initially deep to this latter tendon. At the distal end of the tarsometatarsus the tendon once more becomes deep to the tendon of M. flexor perforatus digiti III, which ensheathes it at this point. The M. flexor perforans et perforatus digiti III tendon in turn ensheathes the branch tendon of M. flexor digitorum longus to the third digit. Near the distal end of the first phalanx, these latter two tendons emerge from the bifurcated end of M. flexor perforatus digiti III and continue distad. At the level of the second phalanx, the M. flexor perforans et perforatus digiti III tendon bifurcates, allowing the branch tendon of M. flexor digitorum longus to continue distad. The two branches of the former tendon insert on the lateral and medial sides of the proximoplar end of phalanx III. The tendon is not ossified.

Comparison.—No interspecific variation was found in this muscle.

Individual variation.—None.

M. flexor perforatus digiti II

M. squamiger.—This elongate, spindle-shaped muscle lies on the lateral side of the crus deep to the distal belly of M. flexor perforatus digiti IV and lateral to M. flexor hallucis longus. The fleshy belly extends nearly one-half of the length of the crus.

Origin.—This muscle arises by a short tendon from the caudal margin of the lateral condyle of the femur, in close association with the tendinous origin of the lateral head of M. flexor hallucis longus, and also by a short branch tendon from the head of the fibula. These two tendinous origins are connected by a ligament that extends over the head of the fibula and from which the fleshy belly of the muscle arises. Despite its outward appearance, there is no direct origin from the head of the fibula. The fleshy belly of this muscle arises about 0.5 mm from the lateral condyle; its muscle fibers run in parallel in the proximal half of the belly.

Insertion.—The fibers of this muscle continue distad to converge on a central tendon that arises along the dorsal surface of the muscle. The tendon passes distad through the tibial cartilage and hypotarsus and down the plantar surface of the tarsometatarsus. Along its length, the tendon is entwined by the M. flexor perforans et perforatus digiti II tendon, which, as they exit the hypotarsus, passes from medial to superficial and then deep to it at the base of the toes. It continues through a canal in the cartilaginous pad at the base of digit II and inserts on the

proximomedial corner of the first phalanx of digit II. It is not perforated here by the tendons of Mm. flexor perforans et perforatus digiti II or flexor digitorum longus. Neither the origin nor the insertion tendons are ossified.

Comparison.—No interspecific variation was found in this muscle.

Individual variation.—A single specimen of *Margarornis squamiger* (LSU 60811) was found to exhibit unilaterally an anomalous fleshy attachment of the belly of this muscle from the fibular shaft. This represents a “singular” variation.

M. flexor perforatus digiti III (FPD3) (Fig. 3)

M. squamiger.—This elongate, spindle-shaped muscle lies deep in the caudal region of the crus, medial and superficial to the medial head of M. flexor hallucis longus.

Origin.—The muscle arises by a short tendon from the intercondyloid region of the femur in common with the medial head of M. flexor hallucis longus and also in association with the origin of the proximal belly of M. flexor perforatus digiti IV. The belly of this muscle arises at about the level of the iliofibularis tendon and extends unipennate for most of the length of the crus; its fibers pass from the origin medially to the tendon of insertion. A somewhat irregular lateral border of the belly of this muscle over the midline of the crus was found to arise from a distolateral expansion of the muscle over the underlying belly of the medial head of M. flexor hallucis longus.

Insertion.—The tendon of insertion arises over the distomedial surface of the muscle. The tendon passes distad through the tibial cartilage and then the hypotarsus, where it loosely ensheathes the insertion tendon of M. flexor perforatus digiti IV. Beyond the hypotarsus, the tendon is joined by the long branch tendon of M. fibularis longus and continues distad to the base of digit III. Along its length, the tendon is entwined by the tendon of M. flexor perforans et perforatus digiti III. As they exit the hypotarsus, the former starts deep, passes superficial, then again deep to the latter tendon at the base of the toes. The tendon bifurcates on the plantar surface of the first phalanx, permitting the passage of the deeper tendons of Mm. flexor perforans et perforatus digiti III and flexor digitorum longus. The branches of the tendon of M. flexor perforatus digiti III insert on either side of the base of the second phalanx and the cartilaginous pad underlying the joint between the first and second phalanges, superficial to the former tendons. Neither the origin nor the insertion tendons are ossified.

Comparison.—No interspecific variation was found in this muscle.

Individual variation.—None.

M. flexor perforatus digiti IV (FPD4) (Fig. 1, 2, 4, 6)

M. squamiger.—This muscle consists of two entirely separate bellies, Pars proximalis and Pars distalis, on the lateral side of the crus. Each gives rise to a separate tendon. The two tendons fuse into a single common tendon of insertion at the distal end of the crus.

Pars proximalis: This strap-shaped, almost parallel-fibered muscle lies superficial to M. flexor perforans et perforatus digiti III on the caudal surface of the crus slightly lateral to the midline, and extends only one-third of the length of the tibiotarsus.

Origin.—The muscle arises fleshy from the intercondyloid region of the caudodistal surface of the femur in common with Mm. flexor perforans et perforatus digiti III and flexor hallucis longus.

Insertion.—At its distal end, along the dorsolateral surface, the fibers of this muscle give rise to a fine, hairlike tendon that extends the length of the crus into the tibial cartilage, where it is joined by the tendon of Pars distalis. This tendon is not ossified.

Pars distalis: This belly is located on the lateral surface of the crus, extending nearly two-thirds of its length. It is roughly spindle shaped and becomes unipennate distally.

Origin.—The muscle arises fleshy from the fascial surface of the underlying *M. flexor perforatus digiti II*, and also from the tendinous sheet shared with this muscle. This aponeurotic sheet arises from the distolateral surface of the femur from a point just proximal to the lateral condyle laterad over the head of the fibula to a point superficial to the branch tendon of *M. flexor perforans et perforatus digiti II*.

Insertion.—At its distal end the fibers of this muscle converge on a tendon of insertion that extends caudomedial over the remaining length of the crus toward the tibial cartilage, where it is joined by the tendon of pars proximalis. There is no ossification.

The common tendon of insertion passes through the tibial cartilage and hypotarsus, continuing down to the lateroplantar surface of the tarsometatarsus to the base of digit IV. Here it ensheathes the branch tendon of *M. flexor digitorum longus* to digit IV, passes distad on the plantar surface of digit IV, and divides into two branches. The smaller branch inserts on the lateral side of the base of the second phalanx. The main branch continues distad, opens ventrally to allow passage of the tendon of *M. flexor digitorum longus*, and inserts deep to the latter at the base of the third phalanx. No ossification was found in the tendon.

Comparison.—No interspecific variation was found in this muscle.

Individual variation.—None.

M. flexor hallucis longus (FHL) (Fig. 9)

M. squamiger.—This large muscle lies in the caudal region of the crus, deep to the individual flexor muscles and superficial to *M. flexor digitorum longus*. It extends for nearly three-fourths of the length of the tibiotarsus and is broadly bipennate in appearance.

Origin.—This muscle arises by three separate heads. The lateral and intermediate heads arise via a wide tendon from the caudolateral surface of the lateral femoral condyle in association with the origin of *M. flexor perforatus digiti II*. The tendon extends distad, lateral to the iliofibularis tendon. The medial head arises from the intercondyloid region at the caudodistal end of the femur. The three heads are discussed separately below.

Lateral head: The lateral head arises directly from the origin tendon discussed above. Its fleshy belly begins just proximal to the level of the iliofibularis tendon (ca. 3 mm from the lateral condyle of the femur) and extends distad. The belly of the lateral head continues distad to a point approximately three-fifths of the length of the crus, where it fuses with the medial head.

Intermediate head: The intermediate head arises fleshy on the medial surface of the origin tendon of the lateral head. The muscle fascicles of this head pass distomedial to the iliofibularis insertion to merge into the medial head at about the midpoint of the crus, forming the deep lateral portion of the medial head belly. Some muscle fascicles from the intercondyloid region of the femur lateral to the origin of the medial head may contribute to this head, obscuring the distinction between the intermediate and medial heads.

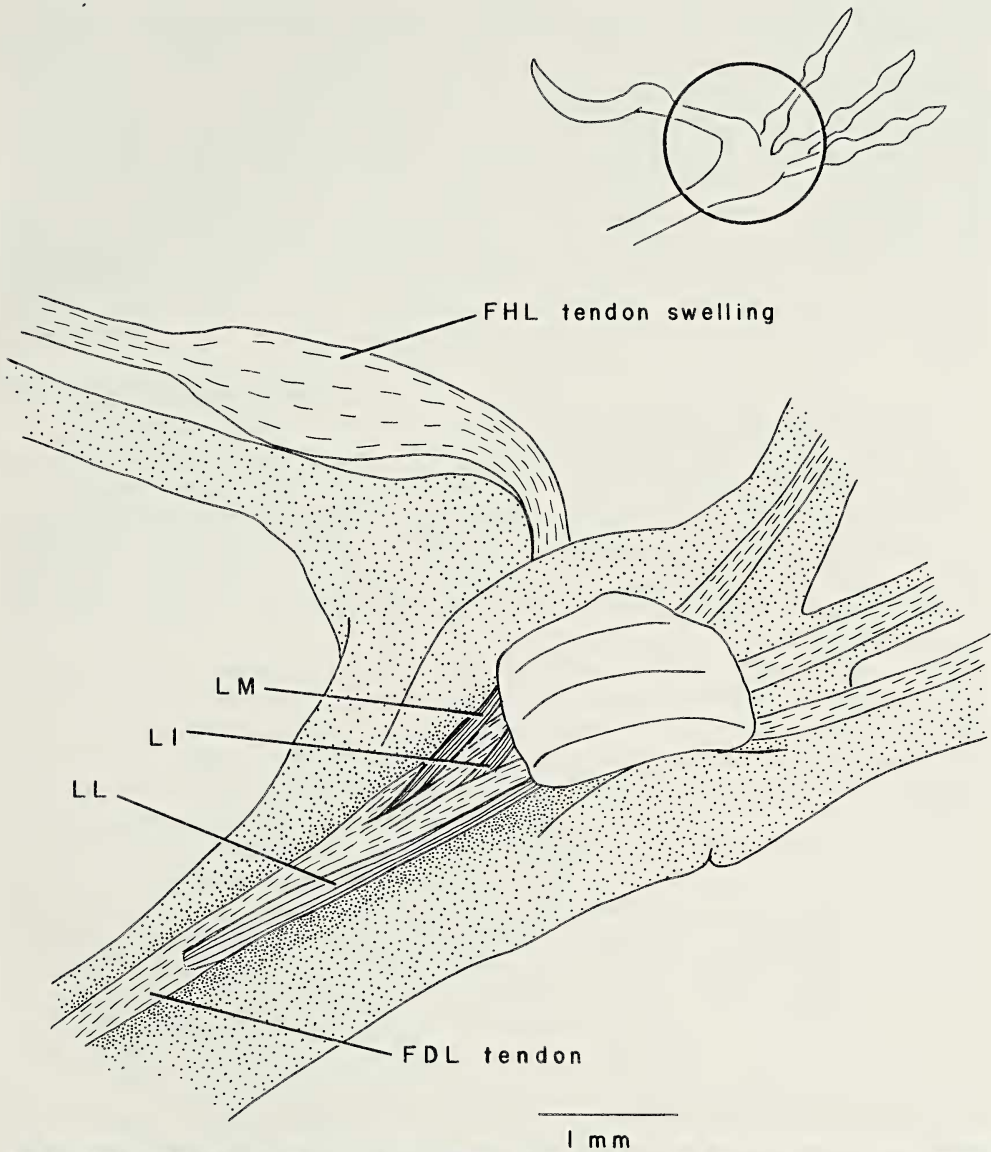


Fig. 9.—View of the hallux illustrating the swelling in the tendon of *M. flexor hallucis longus* (FHL), and also the three bellies of *M. lumbricalis* (L) present in *Premnoplex brunnescens* LSU 70631.

Medial head: The medial head is the largest part of the muscle. It arises fleshy from the medial popliteal region of the femur, becoming tendinous along its medial border in close association with the origin of *M. flexor perforatus digiti III*. The fibers of the medial head extend distad, merging with the intermediate head at about the midpoint of the crus. As it approaches the tibial cartilage, the medial head fuses with the belly of the lateral head to give the muscle an overall bipennate appearance.

Insertion.—The tendon of insertion arises deep within the belly of the muscle, and extends beyond the belly to the deep levels of the tibial cartilage and hypotarsus. It emerges lateral to the insertion tendon of *M. flexor digitorum longus*.

and continues distad along the deep plantar surface of the tarsometatarsus, crossing over the latter tendon on its way to the hallux. There is no connection (plantar vinculum) between these two tendons as in the Eurylaimidae and *Philepitta* (Philepittidae) (Raikow, 1987:24). At the end of the tarsometatarsus, the *M. flexor hallucis longus* tendon passes lateral to Metatarsal I and curves around its trochlea. In the region of the proximal end of the first phalanx of the hallux, the tendon swells noticeably from both dorsoventral and lateromedial perspectives (Fig. 9). This swelling is somewhat harder and darker in coloration than the surrounding tendon, yet does not appear to be mineralized. The tendon then returns to its normal girth and proceeds distad along the plantar surface of digit I to insert at the base of the ungual phalanx. An elastic vinculum arises from the deep surface of the tendon to insert near the distal end of the first phalanx. The tendon is not ossified.

Comparison.—No interspecific variation was found in this muscle.

Individual variation.—None.

***M. flexor digitorum longus* (FDL) (Fig. 7, 8, 9)**

M. squamiger.—This is the deepest muscle on the caudal surface of the crus, lying deep to *M. flexor hallucis longus*. It is composed of a single belly arising by two separate heads from along the shafts of the tibiotarsus and fibula. The belly of this muscle is large and broadly bipennate, extending nearly three-fourths of the length of the crus.

Origin.—The muscle arises by two heads that converge onto a central tendon at a point about two-thirds of the length of the crus. The medial head arises fleshy from the caudal surface of the head and adjoining portion of the shaft of the tibiotarsus, just lateral to *M. plantaris*. This origin is slightly tendinous along its medial border. The slightly smaller lateral head arises fleshy from the caudal surface of the head and shaft of the fibula, and also from the adjacent caudolateral aspect of the tibiotarsal shaft. The lateral head extends distad to join the medial head at about the midpoint of the crus. The fibers of both converge on a common tendon, giving a bipennate appearance to the muscle.

Insertion.—The common belly extends nearly the full length of the crus. A wide, flat tendon of insertion arises along its dorsal surface and passes distad through the tibial cartilage and hypotarsus. It proceeds distad along the plantar surface of the tarsometatarsus to emerge from a position deep to the *M. flexor hallucis longus* tendon. The tendon is ossified for most of the length of the tarsometatarsus, from its emergence from the hypotarsus to its division into three branches. The branch to digit II passes through a deep portion of the cartilaginous joint pulley at the base of the digit and proceeds distad along the plantar surface of the digit to insert at the base of the ungual phalanx. Near its termination, it gives rise to a single elastic vinculum that inserts on the plantar surface of the second phalanx. The branch to digit III inserts on the base of the ungual phalanx, on the plantar surface of the distal end of phalanx III (by means of an elastic vinculum), and on the cartilaginous pad at the proximal end of that phalanx (by an additional, much thinner, hairlike vinculum). The branch to digit IV is ensheathed at the base of the digit by the tendon of *M. flexor perforatus digiti IV*. It then continues distad to insert at the base of the ungual phalanx, producing an elastic vinculum to the proximal end of phalanx IV. This pattern of vinculum insertions corresponds to ABA in Raikow's (1978:25) classification of FDL insertions.

Comparison.—In *Roraimia adusta* (AMNH 7685), an additional vinculum was found to be associated bilaterally with digit IV, corresponding to ABB in Raikow's (1978:25) classification of FDL insertions.

Individual variation.—A single specimen of *Margarornis squamiger* (FM 331197) was found to exhibit bilaterally an additional vinculum like that in *Roraimia adusta*. This same variation was also found in *Premnoplex brunnescens* both unilaterally (LSU 70631) and bilaterally (LSU 75010). Raikow et al. (1990) reported an absence of individual variation in this pattern in two oscine species. In *Margarornis rubiginosus* (LSU 64786), the insertion tendon was unossified bilaterally. Both of these are "singular" variations.

Muscles of the Pes

M. extensor hallucis longus

M. squamiger.—This is a tiny muscle that consists of two parts, Pars proximalis and Pars distalis, which lie on the dorsomedial surface of the tarsometatarsus.

Pars proximalis: This muscle consists of a long, slender belly that is parallel fibered for most of its length. It arises fleshy on the proximomedial surface of the dorsal aspect of the tarsometatarsus, adjacent to the insertion of *M. tibialis cranialis* and medial to the insertion tendon of *M. extensor digitorum longus*. The belly passes distad, extending nearly two-thirds of the length of the tarsometatarsus, before giving rise to a tendon. The tendon of insertion continues distad, curving ventrad along the medial surface of the tarsometatarsus, near the end of which it passes superficial to *Pars distalis* and Metatarsal I. At the base of the hallux, the tendon passes beneath a tiny retinaculum and then passes distad along the dorsal surface of the proximal phalanx to insert at the base of the ungual phalanx in association with an elastic extensor ligament that passes from the proximal to the ungual phalanx.

Pars distalis: This muscle is tiny and narrowly fan shaped and lies at the base of Metatarsal I of the hallux. It arises fleshy from the medial surface of the tarsometatarsus proximal to Metatarsal I, and becomes tendinous as it passes distad. The belly passes distocaudad under a tiny retinaculum adjacent to the tendon of *Pars proximalis* to insert onto the joint capsule at the base of the hallux.

Comparison.—No interspecific variation was found in this muscle.

Individual variation.—None.

Discussion.—This muscle was particularly difficult to dissect owing to its extremely small size and relative resistance to stain. We were able to isolate at least one specimen in each of the five species that had *Pars distalis*; the few cases in which it appeared to be absent were most likely the result of dissection artifact.

M. flexor hallucis brevis

This muscle was absent in all of the specimens dissected.

M. abductor digiti IV

This muscle was absent in all of the specimens dissected.

M. lumbricalis (LL, LM, LI) (Fig. 9)

M. squamiger.—This "muscle" consists of two entirely separate structures, apparently composed mostly of elastic tissue, which arise from the distal end of

the insertion tendon of *M. flexor digitorum longus* just proximal to the latter's trifurcation. Among passerines, this "muscle," when present, normally consists of a single belly (George and Berger, 1966:483–484; Raikow, 1976:789, 1978:25), which appears to correspond to the medial belly described here.

Lateral belly: This is a tiny strap-shaped structure that arises on the ventrolateral surface of the tendon of *M. flexor digitorum longus* at its distal end, just before the point of trifurcation. It extends distad to attach to the proximolateral surface of the connective tissue associated with the joint pulleys of the three forward toes, just lateral to the joint pulley associated with the branch tendon to the fourth digit.

Medial belly: This is a tiny strap-shaped structure, similar to the lateral belly in appearance, that arises on the deep (dorsal) surface of the *M. flexor digitorum longus* tendon at its distal end, just before the point of trifurcation. It extends distad between the branch tendons to the second and third digits to insert on the proximomedial surface of the connective tissue associated with the joint pulleys of these branch tendons. The medial belly is somewhat more slender in appearance than the lateral belly.

Comparison.—In *Premnornis guttuligera* (exceptions: bilaterally, LSU 83865, LSU 89444; unilaterally, LSU 89445) and *Premnoplex brunnescens* (exceptions: bilaterally, LSU 89447; unilaterally, LSU 85962), an extremely slender additional belly was discovered. This hairlike intermediate belly arises from a common origin with the medial belly and extends between the branch tendons of *M. flexor digitorum longus* to the third and fourth digits to insert on the proximal surface of the connective tissue associated with the joint pulleys of these branch tendons, in a manner similar to the medial belly. This intermediate belly apparently arises by appropriation of tissue from the medial belly, which appeared somewhat more slender in appearance, while the lateral belly appeared larger. Its absence in several specimens may be the result of dissection artifact. None of the other birds studied were found to possess a third belly.

Individual variation.—In *Margarornis squamiger* FM 331197, the lateral belly was found unilaterally to extend distomedial underneath the *M. flexor digitorum longus* branch tendon to the fourth digit, continuing distad to an insertion point slightly medial to that found in other specimens. This corresponds to a "singular" variation.

Discussion.—The tissue composing these structures absorbs iodine stain less readily than do other muscles, and perhaps in these species *M. lumbricalis* consists more of connective tissue (perhaps elastic tissue) than of muscle.

DISCUSSION

Scansorial adaptations.—The behavioral ecology of treerunners is not well documented, nonetheless several writers on the subject (de Schauensee and Phelps, 1978:194; Feduccia, 1970:22–3; Ridgely, 1976:197–8; Wetmore, 1972:74, 77) agree with Vaurie that "all the species of [the] *Margarornis* [assemblage] seem to be arboreal and more or less scansorial" (1980:230). Treerunners are often compared with woodcreepers in their scansorial movements and their occasional use of the tail as a brace. Although the members of the *Margarornis* assemblage are considered to be less specialized for the scansorial habit than are woodcreepers, a functional analysis of the modifications to muscles noted above reveals several as adaptations to tree-climbing behavior.

Stolpe's (1932) functional analysis of woodpeckers (Picidae) (reviewed by Bock and Miller, 1959) called attention to an important change in the role of gravity in scansorial forms. In nonscansorial birds, gravity causes flexion of the leg joints; but in vertical climbing scansorial forms, gravity assists the extension of the joints. Stolpe (1932) resolved the force of gravity, acting vertically through the bird's center of gravity, into two components. One acts downward and inward through the axis of the tail, which acts as a brace against the tree trunk. A second is directed downward and outward, and tends to pull the bird away from the trunk. In a tail-supported bird, these forces combine to place the burden of supporting the weight of the bird on the forward toes, while diminishing the importance of flexing the hallux. Winkler and Bock (1976) revised the force analysis, but this does not modify the prediction that with the adoption of scansoriality, flexor muscles in the leg should become better developed, while extensors of the leg and flexors of the hallux might undergo reduction.

The above analysis specifically suggests that treerunners should exhibit modifications that strengthen flexion of the leg elements. *M. iliotibialis cranialis* is thought to flex the femur and extend the crus as a two-joint muscle (Raikow, 1985:104). Its insertion onto the surface of *M. femorotibialis internus* in many Furnariids and other passerines is thought to augment its role in flexing the femur (Raikow, personal communication). This is the condition in treerunners (Fig. 3). The presence of a similar insertion onto *M. femorotibialis internus* in other scansorial birds (e.g., *Certhia americana* (Raikow, personal communication)) and many woodpeckers (Swierczewski, 1977:18) supports the adaptive interpretation of this variation for scansorial behavior. The presence of this insertion in some nonscansorial arboreal furnariines (Raikow, personal communication) suggests that this character is not an adaptation to scansoriality per se, however, but may be a modification for the agile movements associated with arboreal birds in general.

Other character states found in this study may be interpreted as adaptations for flexion of the tibiotarsus. This is brought about primarily by *Mm. iliofibularis*, flexor cruris lateralis, and flexor cruris medialis. *M. iliofibularis* did not vary significantly from its condition in nonscansorial ovenbirds, so in treerunners it shows no adaptation to scansorial life.

M. flexor cruris lateralis in the Dendrocolaptinae and some Furnariinae (Raikow, personal communication) exhibits a partial functional change from extending the femur to flexing the crus. This results from a partial shift in the effective insertion of Pars pelvica from the femur (via Pars accessoria) to the crus (via Tendon M), as shown by the relative size of the tibial lobe on Pars pelvica, the fibers of which end in Tendon M. Raikow (personal communication) distinguishes primitive and derived states for this muscle. The latter is found among most dendrocolaptines and some furnariines. The origin of Tendon M entirely from the tibial lobe in *Premnoplex brunescens* and *Premnornis guttuligera* (Fig. 8) probably reflects this trend, suggesting convergent evolution for this character state. Raikow (personal communication) found that nonscansorial ovenbirds like *Geositta* have the primitive arrangement, while others (*Leptasthenura*, *Synallaxis*, and *Certhiaxis*) have a more derived arrangement. The strength of this trend in dendrocolaptines argues for its adaptive value in flexing the tibiotarsus. As with *M. iliotibialis cranialis*, this change may be useful to agile forms generally and to scansorial types in particular.

The modestly increased origin of *M. flexor cruris medialis* (Fig. 5) may slightly

enhance its function as a flexor of the tibiotarsus. In that case it would represent an adaptation for scansoriality.

Flexion of the tarsometatarsus is brought about primarily by the action of *M. tibialis cranialis*. Since this muscle is no different in treerunners than in nonscansorial forms, it cannot be argued to be specially adapted for scansorial life.

Some of the character states described above may be adaptations for flexion of the digits. This movement is brought about by *Mm. flexor perforans et perforatus digiti II*, *flexor perforatus digiti II*, *flexor perforans et perforatus digiti III*, *flexor perforatus digiti III*, *flexor perforatus digiti IV*, *flexor digitorum longus*, and *flexor hallucis longus*. These muscles show little evidence of specialization for increased strength of digital flexion. The expanded origin of *M. flexor perforans et perforatus digiti II* may aid in the flexion of the second digit. Likewise an additional belly of *M. lumbricalis* might be interpreted as aiding in flexion of the forward toes through its role in maintaining the positions of the joint pulleys, but any such effect would be minimal given the feeble nature of the muscle.

In the other flexors of the forward toes, the situation is even less clear. *Mm. flexor perforatus digiti II* and *flexor perforatus digiti III* did not differ significantly from other passerine birds, nor did *M. flexor digitorum longus* have the femoral head found in woodcreepers (Raikow, personal communication). *M. flexor perforatus digiti IV* in treerunners does vary significantly from its condition in other passerines, yet paradoxically the reduction of *Pars proximalis prima facie* would appear to weaken rather than strengthen flexion in this digit. The ossification of most of the crural tendons found in dendrocolaptines (Raikow, personal communication) may be an adaptation to scansorial life, but is absent in treerunners.

In summary, of several muscle variations found in treerunners, four were found to be possible products of adaptation to scansorial life: (1) the insertion of *M. iliotibialis cranialis* onto *M. femorotibialis internus*, (2) the extended origin of *M. flexor cruris medialis*, (3) the expanded origin of *M. flexor perforans et perforatus digiti II*, and (4) the second belly in *M. lumbricalis*. Altogether, the hindlimb muscles of the treerunners are much less highly specialized for scansorial behavior than are those of the woodcreepers (Raikow, personal communication).

Individual variation.—Raikow et al. (1990) found individual variation in the hindlimb musculature of several passerines to be relatively infrequent and concentrated in a few muscles. Their classification of variation is reviewed above under Materials and Methods.

The significant variations found in the present study are summarized in Table 1. No “incongruous” or “explosive” variations were found. In addition to numerous “minor” variations, five different “singular” variations and two “mimicking” variations were found. Of 620 muscles dissected, only 24 (3.9% of the total) were found to vary significantly. This is similar to the results of Raikow et al. (1990). Most of these variations occurred unilaterally, which corroborates the suggestion by Raikow et al. (1990) of the importance of bilateral dissection to prevent misinterpreting such variants as diagnostic characters in phylogenetic studies.

Passerine monophyly.—Raikow (1982) found three hindlimb muscle states to be synapomorphic for the Passeriformes. Most passerines exhibit the Type VII arrangement of the deep plantar tendons, in which *M. flexor digitorum longus* supplies digits II, III, and IV; *M. flexor hallucis longus* supplies the hallux; and the tendons of these muscles are not connected by a vinculum (Raikow, 1985: 125). The only exceptions are the broadbills (Eurylaimidae) and *Philepitta* (Phile-

Table 1. — Individual variation in hindlimb muscles. Two types of variation, "singular" (S) and "mimicking" (M), are reported (see Raikow et al., 1990). Entries denote the number of specimens of each species found to exhibit the variation: unilaterally (U) and bilaterally (B). See text for discussion. * One of the legs of a member of this series was damaged such that no determination was possible.

Muscles and variations	Types of variations	Species and numbers of specimens examined				
		Margarornis squamiger (S)	Margarornis rubiginosus (2)	Roraimia adusta (1)	Premioplex guttifer (S)	Premiornis brunneus (1)
M. iliotochanteus medius						
a) fusion with ITCR	M	—	—	—	—	1 (B)
M. gastrocnemius pars medialis						
a) absence of patellar band	M	—	1 (B)	—	—	3 (U), 2 (B)
b) presence of separate origin tendon	S	2 (U)	1 (U)	—	1 (U)	—
M. flexor perforatus digiti II						
a) presence of fleshy attachment to fibula	S	1 (U)	—	—	—	—
M. flexor digitorum longus						
a) presence of additional vinculae to digit IV	S	1 (B)*	—	—	—	1 (U), 1 (B)
b) insertion tendon not ossified	S	—	1 (B)	—	—	—
M. lumbricalis						
a) lat. belly extends beneath FDL branch tendon to digit IV	S	1 (U)	—	—	—	—

pittidae), which possess a vinculum between these tendons, and are thus Type I (Raikow, 1987:24). If this is taken to be a derived state, (Raikow, 1987:32–33), then the Type VII arrangement of the plantar tendons is a synapomorphy of the Passeriformes. All specimens of the *Margarornis* assemblage had a Type VII arrangement.

Raikow (1982:440) confirmed that the two bellies of *M. pubo-ischio-femoralis* in passerines, *Pars cranialis* and *Pars caudalis*, are arranged in a cranial-caudal orientation with slight overlap. This contrasts with the condition in nonpasserines, where the muscle is divided into superficial (*Pars lateralis*) and deep (*Pars medialis*) portions. Again, all treerunners exhibited the typical passerine arrangement.

Finally, passerines are characterized by the loss of most of the intrinsic muscles of the second, third, and fourth toes in contrast to nonpasserines (Raikow, 1982: 440–441). These muscles were likewise absent in the treerunners.

In summary, all three of the derived hindlimb myological character states suggested by Raikow (1982) to be synapomorphies of the passeriform clade were found to be present in the birds of this study, further corroborating their use as characters diagnostic of the order.

CONCLUSIONS

The treerunners have a few specializations for scansorial behavior in the flexor muscles of the thigh and crus, and possibly one in a digital flexor. In general, however, their hindlimb muscles are not as highly specialized for trunk climbing as are those of the woodcreepers. Individual variation in treerunner hindlimb muscles is of low frequency, and comparable to that in other passerines studied. Three treerunner hindlimb muscle conditions corroborate the monophyly of the Order Passeriformes.

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